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TWO IMPORTANT INTRODUCED PARASITES OF THE BROWN-TAIL MOTH[1]

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INTRODUCTION

To make clearer the following discussions of two parasites of the brown-tail moth (*Euproctis chrysorrhoea* Linnaeus), a brief summary of the introduction and life cycle of the host species is given here. The brown-tail moth was introduced accidentally from Europe about 1890, probably on nursery stock, and made its first appearance in the vicinity of Boston, Mass. It increased rapidly and soon became widely distributed, extending its ravages over very nearly all New England, and also became established in portions of New Brunswick and Nova Scotia. The destructiveness of the species has diminished very markedly during the past few years, however, due in large part to natural control agents.

The brown-tail moth deposits her eggs during the latter part of July, in an elongate mass of several hundred on the underside of a leaf, commonly of apple (*Malus sylvestris*), pear (*Pyrus communis*), oak (*Quercus* spp.), or wild cherry (*Prunus* spp.), and covers them with a dense layer of brown hair taken from the tuft at the posterior end of her body. These eggs hatch after from two to three weeks and the very small pale brown caterpillars begin feeding in a colony on the terminal leaves, which they tie together with a large amount of fine silk to form a firm web 3 or 4 inches in length. For a considerable period in the early autum the caterpillars feed slightly, coming out of their webs for this purpose from time to time; their growth is very slow, however, and although they molt once or twice they do not attain a length of more than 4 or 5 mm. before becoming dormant for the winter. In the early spring, with the opening of the buds, the caterpillars leave their webs and begin feeding,

[1] The investigations which form the basis for this article were conducted at the Gipsy Moth Laboratory, Melrose Highlands, Mass., under the general direction of Mr. A. F. Burgess. The writer wishes to acknowledge the assistance received from Mr. S. S. Crossman, of the Laboratory, and from many others of the staff who have helped in various phases of the work. The photographs were taken by Mr. H. A. Preston. Determinations of chalcidoid hyperparasites were made by Mr. D. W. Jones, of this Station, and Dr. Robert Matheson, of Cornell University.

still in colonies, near the winter web. But as they become larger they crawl to various parts of the tree or even to different trees nearby, feeding ravenously; they attain their growth about the middle of June, and are then 1½ inches in length. Pupation takes place within loosely spun cocoons fastened in leaves that have been drawn together from the sides, in crevices of the bark, in stone walls, and in other protected places. The moths, issuing after about three weeks, mate, and the females begin depositing their eggs. There is only one generation a year.

IMPORTATION OF THE PARASITES

In the winter of 1905–6, following the first visit by Dr. L. O. Howard, Chief of the Bureau of Entomology, to Europe for the purpose of arranging for the sending to New England of parasites of the gipsy and brown-tail moths, large numbers of the winter webs of the latter species were received at the parasite laboratory, then located at North Saugus, Mass. These webs were placed in special cages, one of which is shown in Plate 19, A. The cage consisted of a large wooden box, capable of holding about 1,000 webs of the brown-tail-moth caterpillars, and having a number of glass tubes projecting from the upper half of one side. Any parasites issuing from the webs would be attracted into the tubes by the light.

Very early in the spring many individuals of *Pteromalus egregius* Foerster, a chalcidoid external parasite of the wintering brown-tail moth larvæ, and also many specimens of *Monodontomerus aereus* Walker, another chalcidoid, that frequently hibernates as an adult in the brown-tail web, entered the tubes. Shortly the brown-tail-moth caterpillars in the cages became active and made their way into the glass tubes; as these became filled, the caterpillars were removed and destroyed, since the probability of their harboring internal parasites seemed slight. However, Mr. E. S. G. Titus, at that time in charge of the work, fed a few of the caterpillars for a time, as an experiment, and secured from them representatives of two parasitic species, both braconids, one of the genus Apanteles and the other belonging to the genus Meteorus. It is these two species with which this paper deals.

REARING AND COLONIZATION OF THE TWO PARASITES

As a result of the discovery by Mr. Titus, the caterpillars from the webs received during succeeding winters were not destroyed upon issuing in the spring, as had been done previously, but were fed for several weeks, so that any internal parasites might be reared. For rearing methods and types of cages used, see Howard and Fiske (*1*).[1] This was continued until 1911, when importations ceased, with the result that some 40,000 cocoons of *Apanteles lacteicolor* and about 1,600 of *Meteorus versicolor*

[1]Reference is made by number (italic) to "Literature cited," p. 205.

were obtained for liberation in brown-tail-moth infestations. That these species are widely distributed in Europe was shown by the recovery of both parasites from webs that had been sent from the following countries: France, Netherlands, Germany, Russia, especially southern Russia, Austria, Switzerland, and Italy. Once introduced into New England, both species became quickly established, so that after 1911 a large amount of material for colonization was obtained from caterpillars collected in local infestations. So rapid has been the spread of the parasites that, although up to the present only 150 colonies of the Apanteles and 20 of the Meteorus have been placed in 135 and 18 towns, respectively, no further colonization is necessary. Both parasites have been recovered from practically the entire brown-tail moth area, either by rearing from the brown-tail moth larvæ in the early spring or by dissection from hibernating caterpillars.

In making collections of brown-tail-moth webs for the recovery of these parasites and to obtain material for colonization, whenever possible 105 webs have been taken in each of a considerable number of towns some time during the winter and placed in cold storage until spring. One hundred of these were then placed in one of the large rearing trays (Pl. 19, B), and the caterpillars fed. The foliage was placed upon mosquito netting that had been laid over the webs. The purpose of this was to draw the caterpillars away from their webs, so that the latter could be removed readily and destroyed by rolling back the netting with foliage and larvæ. This greatly facilitated the picking over of the webs for the cocoons of the parasites. The remaining five webs were placed in small individual trays (Pl. 19, C). The caterpillars in each of these single-web trays were counted, and since a count of the Apanteles and Meteorus cocoons removed later was also made, the extent of parasitism by these two species at each locality was determined.

When dissections were made for the recovery of the parasites, as in 1917 and 1918, the work was done early in the year while the caterpillars were still dormant. In 1917, the first year of systematic dissection work for the recovery of brown-tail-moth parasites, 5 webs were taken from each of the collections that had been made the preceding fall or during the winter; from each of these webs 50 caterpillars were taken at random and dissected under the binocular microscope. Later it seemed that dissecting a smaller number of caterpillars from a larger number of webs would give a better representation of actual parasite conditions. Accordingly, this year (1918) 20 brown-tail-moth larvæ were dissected from each of 10 webs. This method of determining the extent of parasitism by making dissections probably gives more accurate data than rearing, since the somewhat unnatural conditions under which the caterpillars are fed in the spring must prevent the issuance of some of the parasites. Moreover, the dissections give data on the extent of

competition between the different parasitic species hibernating in the brown-tail-moth larvæ. Still other information obtained by opening the webs and dissecting caterpillars is that on "winter-killing" among the brown-tail-moth larvæ, and the relation of parasitism to this phenomenon. Very low temperatures act as an important control agent in the more northern parts of the brown-tail-moth area in Maine, New Hampshire, Vermont, and parts of Massachusetts. It might be expected that caterpillars infested by parasites would succumb more quickly to the cold, and that thus the low temperatures would act as a proportionately greater check upon the parasites than upon the brown-tail moth larvæ. Fortunately this does not appear to be the case. The parasitism in webs containing a large percentage of dead caterpillars is scarcely, if at all, less than in webs from the same locality with few dead larvæ. Dead caterpillars, as found in the webs, are usually dried up and unfit for dissection, but when dissections have been possible the dead larvæ showed no abnormally great parasitism. The probable reason for this is that the hibernating parasites are very small and have made no great inroads upon the reserve food of the host larvæ, their feeding having been slight at most and extended over a considerable period, so that the caterpillars have not been materially weakened.

APANTELES LACTEICOLOR VIERECK

The species of Apanteles that hibernates in the young caterpillars of the brown-tail moth was described by Viereck in 1911 (*7, p. 475*) from material reared at the Gipsy-Moth Laboratory, Melrose Highlands, Mass., as "*Apanteles lacteicolor*." That so widespread and so general a parasite of the brown-tail-moth caterpillars in Europe should not have been described before is somewhat surprising, and it may yet be found that the insect has been described, but too imperfectly to be recognized thereby. Meanwhile the name "*Apanteles lacteicolor* Viereck" must stand.

As Viereck's description is very brief, a fuller characterization is given herewith.

MALE AND FEMALE.—Length 2.5 mm. Black; head including the antennæ black, covered with a short sericeous pubescence; vertex, front, face, and clypeus all finely punctate; eyes hairy; female antennæ as long as the body, those of the male longer.

Thorax: Mesoscutum densely, rather deeply punctate; scutel more shining, with sparse very shallow punctures, slightly convex; tegulæ black. The propodeum is very distinct from that of other species of the genus in that it has on the apical two-thirds three, one median and two lateral, large shining areas, and a less distinctly margined and less smooth almost circular area on each side near the base; the median area is pentagonal, while the apical lateral areas are subtrapezoidal, and extend slightly beyond the apex of the median area, reaching the posterior margin of the propodeum. The wings have the veins generally pale, with the costa and stigma brown in the female and only the outline of the stigma brown in the male; the exterior vein of the first cubital cell is only slightly angled a little below the middle. Legs:

The anterior pair have the coxæ black, the trochanters and extreme base of the femora dusky, the remainder of the femora, the tibiæ, and the tarsi yellowish; the middle legs have the coxæ, the trochanters, and the basal two-thirds of the femora black, and the apical half of the tibiæ dusky, the base of the tibiæ and the tarsi yellow; the posterior pair have the coxæ, trochanters, femora, and the apical half of the tibiæ black, and the tarsi blackish, except the extreme base of the basal segment, which is yellowish.

Abdomen: Somewhat shorter than thorax, entirely black; first and second tergites coarsely rugose; the first long, scarcely wider at apex than at base, and usually with a small, indistinct, shining median fovea on its apical half; the second tergite is transverse, three to four times as broad as long down the middle, the posterior margin arcuate; the broad lateral membranous margins on the apical one-third of the first tergite, and along the second blackish; third tergite and beyond smooth and shining. The ovipositor is long, almost half as long as the abdomen.

SEASONAL AND LIFE HISTORY OF APANTELES LACTEICOLOR

THE EGG

The female of *Apanteles lacteicolor* (Pl. 20, A) oviposits in first and second stage brown-tail-moth caterpillars during the month of August. The very small larvæ, those being but two or three days from the egg, are preferred, often being attacked while still on the egg cluster, before they have fed at all. The egg of the parasite (Pl. 20, B) is a minute transparent object, measuring but 0.35 mm. in length, including the stalk at the end opposite the micropile. No particular part of the body of the host is selected for oviposition, the attack being merely a nervous thrust, requiring about one second, into any part of the caterpillar. Only a single egg is deposited at one oviposition, and usually only one egg is placed in a caterpillar. The parasite will oviposit from a dozen to 25 times in quick succession if hosts are available, and will then rest for a period, sometimes for a day or two, before depositing more eggs. Oviposition may extend over a period of several weeks, and a single female may attack upwards of 300 caterpillars, although under field conditions the average appears to be much lower, probably due in large part to the fact that the insect is delicate and rather short lived. In the laboratory one female, over a period of two weeks, oviposited in 320 larvæ, placing two and even three eggs in some of these. That an egg was being deposited with each thrust of the ovipositor was determined by dissecting from time to time caterpillars that had been attacked by the parasite.

HIBERNATING LARVA OF APANTELES LACTEICOLOR

The egg of *Apanteles lacteicolor*, having increased somewhat in size, hatches after about three days, and the young parasitic larva, free in the body cavity of its host, feeds slightly on the fat and lymph there, merely keeping pace with the very slow development of the caterpillar prior to hibernation. The position of this first-stage larva within its host varies, but more commonly the young *A. lacteicolor* is found in the posterior half of the body. As dissected from the hibernating

brown-tail-moth caterpillar, the Apanteles larva is minute and transparent, slightly less than 0.5 mm. in length, and possessing at its caudal end a curious bladder-like organ, commonly referred to as the anal vesicle, and beneath this a prominent fleshy horn projecting downward. On the dorsum of each of the last nine segments of the body is a transverse row of very indistinct, short, though rather stout, backward-projecting spines. When first removed from the caterpillar, the position usually taken by the parasitic larva is that shown in Plate 20, C, the body being curved so that the caudal horn touches or passes across the head. In this stage no tracheal system is visible.

ANAL VESICLE OF APANTELES LACTEICOLOR

The parasitic larvæ of the subfamily to which this species belongs, the Microgasterinae, have at the caudal end of the body a bladder-like structure, called the "anal vesicle," which has been the subject of much discussion, particularly in Europe, by such entomologists as Kulagin, Seurat, and Weissenberg. Weissenberg (*8, 9*), working principally on *Apanteles glomeratus* Linnaeus, formed a number of conclusions on the structure and function of the organ and summarized very well all the work that had been done upon this subject, besides giving the results of his own investigations. It has been determined definitely that the anal vesicle of these larvæ consists merely of a portion of the hind gut which has been evaginated; all but the extreme posterior part of this section of the intestinal tract is concerned, being turned inside out so that the blind end of the midintestine is on the outer ventral surface of the vesicle. The vesicle is present in all endoparasitic stages of *Apanteles* spp., but is reinvaginated very shortly before the larva issues to spin its cocoon. Its function is not so definitely known, but there seem to be two important uses. The fact that the tracheal system of the parasite is not developed until the last endoparasitic stage, when the vesicle begins to be retracted, strongly suggests respiration as an important function, and the delicate structure of the organ would emphasize this. Frequently, when dissecting brown-tail-moth caterpillars during the winter, the writer has found hibernating first-stage larvæ of *A. lacteicolor* in which the hind intestine was not at all evaginated but could be distinctly seen within the larva (Pl. 20, C). On several occasions while such a larva, placed in a drop of water, was under observation, the hind intestine was seen to be slowly pushed out through the anal opening to form the vesicle. While inactive within the host and under a comparatively low temperature, the respiration of the parasite is reduced to the minimum, and the slight respiration that does take place may go on through the body wall. When removed from the caterpillar and placed in water, the parasite becomes active and respiration increases. That at this time the vesicle should be formed supports the theory that an important function of the anal vesicle is respiration. However, Weissenberg (*9*) thinks, as a result of

a series of homologues with the intestinal tracts of other parasitic larvæ, that a yet more important function is excretion. For the present the matter must rest here, but further study may throw more light upon the function of this curious structure.

COMPETITION WITH OTHER PARASITES WINTERING IN THE BROWN-TAIL-MOTH CATERPILLARS

Since there are two other parasitic species that pass the winter within the small brown-tail-moth caterpillars there is naturally some competition between the three. These other species are *Zygobothria nidicola* Townsend, a fly of the family Tachinidae, and *Meteorus versicolor* Wesmael, the other parasite discussed in this paper. It was determined from over 13,000 dissections of hibernating brown-tail-moth caterpillars that whenever *A. lacteicolor* enters into competition with either or both of these species it wins out; the other parasite or parasites present are killed before midwinter, evidently as the result of some toxic action induced by the Apanteles larva. Even when two larvæ of *A. lacteicolor* occur in the same host, only one of these normally completes its development. Some very interesting cases of competition were encountered in the course of the dissecting: In one caterpillar were found two larvæ of *A. lacteicolor*, one of them dead, five dead Zygobothria maggots more or less encysted and no longer occupying their normal position in the fore intestine of the caterpillar, and three eggs of *Meteorus versicolor*, the development of which had been arrested; another caterpillar contained a living larva of *A. lacteicolor*, nine dead Zygobothria maggots, and one partly developed egg of *M. versicolor*, the embryo dead. Many similar cases were encountered, but in no case was a dead Apanteles larva found in the same caterpillar with a living larva of some other parasitic species. This ability to win out over the species of parasites hibernating within the brown-tail-moth caterpillar strengthens considerably the position of *A. lacteicolor*.

LATER ENDOPARASITIC LIFE

In May, when the brown-tail-moth caterpillars resume feeding, the small larvæ of *A. lacteicolor* within these caterpillars likewise become active and begin in earnest the task of destroying their hosts. The parasitic larva develops very rapidly; after a day or two of feeding it attains the length of 1 millimeter, or slightly more (Pl. 20, D), and passes into the second stage, which differs from the first principally in that the mandibles, or structures corresponding to the mandibles, are bidentate and not chitinized, whereas in the first stage they were simple and heavily chitinized (Pl. 20, E). The anal vesicle is much more in evidence, being proportionately larger, but the horn beneath, so prominent in the first stage, is scarcely noticeable, not having increased in size at all. The almost invariable position of *A. lacteicolor* now is in the posterior half of the body of its host, the parasite being longitudinally disposed, its

head directed toward the caudal end of the caterpillar. After 2 or 3 days the parasite passes into the third stage (Pl. 21, A); the mandibles of this stage differ markedly from those of either of the other stages, being much longer and pectinate (Pl. 20, E). In the third stage the larva possesses a tracheal system, not evident before. In this stage, too, the anal vesicle begins to be reinvaginated, being gradually drawn back into the body of the larva, so that, when the parasite issues, no vesicle can be seen.

The infested brown-tail-moth caterpillars are very noticeably retarded and do not get beyond the stage in which they hibernated. Death occurs in from 7 to 12 days after they have begun feeding, and very shortly the full-grown parasitic larva issues.

The species of Apanteles commonly do not kill their hosts upon issuing, the latter sometimes remaining alive two weeks or more. The death of the victims of *A. lacteicolor* then, just prior to issuance of the parasite, is interesting. Just how this death of the host is brought about is not certainly known; but the writer found, on dissecting caterpillars from which this parasite had just issued, that the central nervous system in the posterior part of the body was entirely destroyed, while in various caterpillars, still living, deserted by other species of Apanteles, no such injury had taken place. That in the former case destruction of the nervous system occurs not more than a few hours before the issuance of the parasite, was determined as the result of dissecting a number of brown-tail-moth caterpillars containing *A. lacteicolor* larvæ almost ready to issue, these caterpillars being still alive; the nervous system in these cases had not yet been injured. It seems very probable, after these observations, that the destruction of the nervous system by the larvæ of *A. lacteicolor* is responsible for the early death of the hosts of this parasite.

COCOON OF APANTELES LACTEICOLOR

Directly upon issuing from its host, the larva of *A. lacteicolor* begins spinning its cocoon, completing this after three hours or more. The process of spinning consists of a continuous looping of the silken thread as this is spun out, and a careful fastening of these loops; the larva finds it necessary, in the course of this work, to reverse its position many times. When complete the cocoon is pure white, oblong-cylindrical in form, 4 to 4.5 mm. in length, and surrounded by a small amount of loose silk. The cocoons of the wintering generation are commonly found in the webs of the brown-tail moth caterpillars, while those of the summer generations occur on the underside of leaves, in crevices of the bark, etc.

Changes within the cocoon are rapid. From 18 to 24 hours after spinning has ceased, the waste matter that has accumulated in the midintestine during endoparasitic life (the caudal end of the midintestine is closed during this period) is excreted and is forced to the end of the cocoon. Pupation takes place about 48 hours after the larva has ceased

spinning, and the old larval skin is pushed back upon the excrement previously voided. Gradually the pupa (Pl. 21, B), yellowish white at first, blackens; then the pupal skin is cast, and the adult parasite emerges after first cutting out a perfectly circular lid at one end of the cocoon. The total length of the period spent within the cocoon is from 5 to 8 days.

The adults of the first generation of *A. lacteicolor* are found issuing from about the 20th of May to the middle of June in New England. Mating will take place almost at once, within 24 hours after emergence, and oviposition may begin within 48 hours. Laboratory experiments have shown females of this species unwilling to oviposit during the first 24 hours, but they will do so very readily shortly after this. As is true with many parasites, fertilization is not necessary for reproduction, but unfertilized females produce only males.

SUMMER HOSTS OF APANTELES LACTEICOLOR

Considerable effort has been expended by the writer to determine in what hosts this parasite passes the summer. The species has been reared frequently from small gipsy-moth caterpillars at the laboratory, and Howard (*2, 3*) emphasized the importance of the parasitism upon this species. The writer's observations in the field and experiments at the laboratory have convinced him that wherever brown-tail-moth caterpillars occur in sufficient numbers to insure the presence of a fair proportion of *A. lacteicolor*, the parasitism upon the small gipsy-moth caterpillars is considerable. These are attacked in the first or second stage and are killed by the parasite before they have passed the third (Pl. 21, C). They are greatly retarded in their development when infested by the Apanteles, and when the development of the parasite is nearly complete, the caterpillars seek places of concealment on the lower side of leaves and limbs, in crevices of the bark, etc. Hence they are easily overlooked by men collecting caterpillars to determine the extent of parasitism. So far as the writer has been able to determine, the gipsy moth is the only host, acceptable to *A. lacteicolor*, which is available at the time of the appearance of the adult parasites of the first generation. Where the gipsy moth does not occur the Apanteles females evidently do not oviposit for several weeks, until various native host species, which this parasite will attack, appear. One much retarded caterpillar of *Malacosoma americana* Fabricius was attacked by *A. lacteicolor*, but no reproduction was secured, although, as was found later by dissection, an egg had been deposited. This species is normally too far advanced by the time of the appearance of *A. lacteicolor* to serve as a host of this parasite.

The total period required for the development from egg to adult, in the case of the summer generations, averages 19 to 20 days, and it is during the last weeks of June and in early July that adults of the brood on the gipsy-moth caterpillars emerge.

Between this date and the time of oviposition in the hibernating caterpillars of the brown-tail moth there is a period of more than a month, or ample time for another generation. Furthermore, at this time there are in the field a number of species that would seem to be desirable hosts, including the caterpillars of *Hemerocampa leucostigma* Smith and Abbot, *Notolophus antiqua* Linnaeus, *Datana ministra* Drury, *Hyphantria cunea* Drury, *Apatela hasta* Guenée, and others. Experiments have been carried on in the laboratory with a number of known and unknown species, the caterpillars being reared from eggs and hence parasite-free at the time of their subjection to *A. lacteicolor.* In addition, field collections of first and second stage larvæ of various possible host species have been made, and these reared for the recovery of the Apanteles. In the laboratory reproduction has been secured upon *Apatela hasta* Guenée, *Schizura unicornis* Smith and Abbot, *Hemerocampa leucostigma* Smith and Abbot, and an undetermined arctiid. First-stage larvæ of *Apatela hasta* were very eagerly attacked by *Apanteles lacteicolor*, as were also first-stage larvæ of the *Schizura unicornis* and of the undetermined arctiid. In 1910 *A. lacteicolor* was recovered in the field from *Datana ministra* and *Hyphantria cunea* (*1, p. 289*), and during the past summer the writer has recovered it from *Apatela hasta*, a noctuid not uncommon upon wild black cherry and the species upon which *A. lacteicolor* reproduced so readily in the laboratory. Further evidence of the probable importance of *Apatela hasta* as a host of *A. lacteicolor* was the collection of cocoons of the parasite, during the last week of July, upon wild black cherry where only *A. hasta* was present in numbers. This species can be found in virtually all stages throughout the month of July, and, to judge from observations in the field and laboratory, the writer believes it to be an admirable host for tiding *A. lacteicolor* over the period elapsing before the brown-tail-moth caterpillars that are to carry the parasite over the winter become available.

ECONOMIC IMPORTANCE OF APANTELES LACTEICOLOR

As a control agent *A. lacteicolor* must take high rank. First, it is a very effective parasite of the brown-tail moth, as high as 20 to 25 per cent of the larvæ of a web often being parasitized by this species. Then the facts that there are several generations annually, and that it is a parasite of more or less importance upon the gipsy moth and upon certain native injurious species, add to its value. In addition, *A. lacteicolor* destroys its hosts in the early stages, and thus prevents any considerable feeding by the individuals parasitized, since these are very greatly retarded. Plate 21, D, shows a parasitized and an unparasitized caterpillar of an undetermined arctiid hatched on the same day from the same egg mass and similarly fed. Actual measurements in a number of cases showed that the individuals parasitized by *A. lacteicolor* eat, on the average, about one-fourth as much foliage as caterpillars of the same species and the same

age not parasitized. These factors combine to make *A. lacteicolor* a parasite of considerable importance.

The weak point in the life cycle of the parasite is its evident dependence upon the brown-tail moth for hibernation. This species is now on the decadence, and with it *A. lacteicolor* is becoming less abundant, thus reducing very materially the parasitism upon the gipsy moth and native hosts.

SECONDARY PARASITISM UPON APANTELES LACTEICOLOR

Since the cocoons of the first generation of *A. lacteicolor* occur for the most part within the webs of the brown-tail moth, they are protected from secondary parasitism to a great extent, and a very small percentage of these cocoons is parasitized. Those of the later generations, however, are more accessible to secondaries, and among these parasitism runs quite high. The hyperparasitic species reared from *A. lacteicolor* include the following: *Monodontomerus aereus* Walker, *Pteromalus egregius* Foerster, *Dibrachys boucheanus* Ratzeburg, *Dimmockia* sp., *Habrocytus* sp., *Pezomachus* sp., and two species of Hemiteles.

METEORUS VERSICOLOR WESMAEL.

The species of Meteorus wintering in the hibernating brown-tail-moth caterpillars was described by Wesmael in 1835 as "*Meteorus versicolor*." It is an extremely variable form, and a number of varieties, which may or may not be good, have been founded on color differences. Following is a redescription of the species based on the examination of many specimens bred from European as well as from local material.

Length 3.5–5 mm. General color honey-yellow; however, there is great variation in color: Some specimens are entirely yellowish, with no black markings whatever; while others have the propodeum and most of the dorsum of the abdomen black; all gradations between these forms can be found.

Head transverse, yellow; antennæ yellowish to brownish; eyes bluish to black; stemmaticum sometimes black; mandibles yellowish, except the extreme tips, which are brownish; palpi yellowish.

Thorax: Mostly honey-yellow; prothorax, mesothorax, and scutellum yellow, except occasionally the lobes of mesothorax dusky; the mesothoracic lobes feebly punctate, the parapsidal grooves broad, well marked, and ending posteriorly in a broad, depressed, roughened area, which extends to the apex of the mesoscutum; suture at base of scutellum deeply foveate. Propodeum variable, but usually at least somewhat discolored, and often entirely blackish; metapleuræ deep honey-yellow, even when propodeum is entirely black; propodeum not sloping from base to apex, the posterior declivity abrupt. Wings: Base of the costa brownish, the rest of the veins and the stigma pale; cubitus beyond the second cubital cell subobsolete; the second cubital cell quadrate; recurrent vein variable, entering the first cubital cell or interstitial with the first transverse cubitus. Submedian cell very distinctly longer than the median. Legs: Entirely honey-yellow, except sometimes slightly dusky on the apex of the hind coxæ, the apex of the hind femora, the apex of the hind tibiæ, and the hind tarsi.

Abdomen: Not or scarcely longer than the thorax; varying from entirely yellowish to largely blackish; segment 1 is longitudinally aciculated on the apical half, and does

not possess the elongate fossæ found in some species of the genus; segment 2 and beyond very smooth and shining; segment 1 nearly as long as the remainder of the abdomen; its basal half always pale yellowish, its apical half usually blackish, except extreme apical margin which is yellowish; the second segment commonly with a large blackish or brownish spot on each side, the two occasionally merging, but usually leaving the middle of the segment yellow; beyond the second segment the abdomen is more or less blackish, sometimes entirely black. Ovipositor about one-half the length of the abdomen.

SEASONAL AND LIFE HISTORY OF METEORUS VERSICOLOR.

THE EGG.

Like *Apanteles lacteicolor*, *M. versicolor* oviposits in the small brown-tail-moth caterpillars during August and early September. Like *A. lacteicolor*, too, *M. versicolor* deposits only a single egg with each thrust of the ovipositor, although a number of caterpillars may be attacked within a very few minutes. Oviposition by this species is very deliberate. The parasite (Pl. 22, A), slowly bending the abdomen downward and forward so that the ovipositor is parallel with the venter and projects between the anterior legs, advances stealthily toward her victim. On reaching the larva she remains perfectly motionless for a moment or two, apparently waiting for the caterpillar to make some movement; then, with a quick forward thrust, she inserts the ovipositor, and almost at once withdraws it again, having left an egg in the body of the caterpillar. The egg (Pl. 22, B) is a minute, pale brownish-yellow, oval body, about 0.2 mm. in length, with a prominent stalk, 0.1 mm. long, at the end opposite the micropile; the surface is marked off in minute hexagonal areas. It increases much in size, until 5 or 6 days after deposition, when the larva is ready to issue (Pl. 22, C), it measures 0.6 to 0.75 mm. in length, exclusive of the stalk, which has not increased in size, and about 0.55 mm. in breadth. Shortly before it is ready to issue from the egg the larva of *M. versicolor* becomes very active, as can be observed easily under magnification, the chorion now being transparent. After lashing about with its long caudal appendage for some little time, it finally breaks out and floats free in the body cavity of its host.

HIBERNATING LARVA OF METEORUS VERSICOLOR

At the time the larva issues from the egg its total length is about 1.5 mm. The striking features of this stage are the long caudal horn, 0.6 mm. in length, and the large, brown, heavily chitinized head capsule containing a pair of strong curved mandibles. The caudal appendage is merely a fleshy extension, obviously to aid the larva in getting out of the egg and later in locomotion. It does not have the significance of the anal vesicle of the larva of *A. lacteicolor*, for in *M. versicolor* there is no need of a special respiratory device, the tracheal system being already developed in the first-stage larva. This larva feeds very slightly in the fall, increasing scarcely at all in size, and passes the winter in the

first stage within the body cavity of its host. So far as the writer has been able to determine, *M. versicolor* hibernates only in the brown-tail-moth caterpillars in New England.

When dissections were being made of hibernating brown-tail-moth larvæ in late winter, partly developed eggs of *M. versicolor* were often found, and the writer at first supposed that the species occasionally might go through the winter in this way. But later it was observed that always, when such an egg is found in a hibernating brown-tail-moth caterpillar, there occurs with it a first-stage larva of *A. lacteicolor*. The latter was evidently there first, and was able to prevent the complete development of the egg of *M. versicolor*, perhaps through the secretion of some toxic substance which killed the embryo. That the embryo is actually dead can usually be determined on close examination, provided that development has gone sufficiently far.

LATER ENDOPARASITIC STAGES OF METEORUS VERSICOLOR

In the spring when the brown-tail-moth caterpillars begin feeding the larvæ of *M. versicolor* within some of them also become active, and after from 10 to 14 days the cocoons of the parasite appear. Development of the larva is not as rapid as in the case of *A. lacteicolor*, for the feeding of the parasite does not prevent the host from molting once in the spring. The first-stage larva of *M. versicolor* attains a total length of about 2 mm. and passes into the second stage about 3 days after resuming activity. The second-stage larva no longer possesses the brown, heavily chitinized head capsule and the strong curved mandibles; the mandibles, or what correspond to the mandibles (Pl. 22, D), are exceedingly difficult to find, not being chitinized. The anal appendage, too, is no longer so much in evidence. The length reached in this stage is about 4 mm., and the duration of the stage is about 4 days. The third stage, extending over a period of from 2 to 3 days, differs from the preceding stage principally in that the mandibles are chitinized, the anal appendage is reduced to a short spur, and the size is slightly larger. When full grown (Pl. 21, E) the parasite measures 5 to 6 mm. in length, is cylindrical, and yellowish. It does not kill its host before emerging, as does *A. lacteicolor*, but leaves the latter to writhe for 24 hours or more.

COCOON OF METEORUS VERSICOLOR

Unlike *A. lacteicolor*, the larva of *M. versicolor* does not begin spinning at once on issuing from its host, but commonly crawls some little distance along a twig or branch and then, suspending itself by a strong thread, which it has spun and made secure, forms its cocoon, which is elongate-oval but somewhat attenuated at both ends, and brown. Within the cocoon the head of the parasite is directed downward; the excrement which accumulated during endoparasitic life is pushed to the upper end about 36 hours after spinning has ceased, and a day or two

later the last larval skin is pushed back upon this. The pupal period requires from 4 to 6 days, bringing the total time spent within the cocoon to from 7 to 9 days. The emergence of the adult is through an opening made by cutting off a circular lid at the lower end; thus the cocoon is left hanging in mid-air, even after the parasite has gone (Pl. 21, G). Scheidter (*5*) in recording his observations on *M. versicolor* in Europe, states that the period from the issuance from the host to emergence from the cocoon is 13 to 14 days, while the pupal period alone is 9 days; but in no case that has come under the writer's observation has the period spent within the cocoon been as long as this.

SUMMER HOSTS OF METEORUS VERSICOLOR

The adults of the first generation emerge during the first two or three weeks of June. Mating takes place very soon after issuance, and the females begin ovipositing. Here, again, fertilization is not necessary for reproduction, but, as is true with *A. lacteicolor*, unfertilized females produce only males.

In Europe Schmiedeknecht (*6, p. 223*) records *M. versicolor* from the following hosts: *Laria v-nigrum* Müller, *Asteroscopus sphinx* Hufnagel, *Bombyx neustria* Linnaeus, *B. lanestris* Linnaeus, *Triphaena pronuba* Linnaeus, *Geometra papilionaria* Linnaeus, *Eupithecia exiguata* Hübner, and *Argyresthia nitidella* Fabricius. In New England the adult parasites of the first generation evidently prefer the last two stages of the brown-tail-moth caterpillars for oviposition. Only occasionally are gipsy-moth caterpillars attacked by this species; *M. versicolor* oviposits very eagerly in *Hemerocampa leucostigma* and *Notolophus antiqua*, however; *Hyphantria cunea* has also been recorded as a host (*1, p. 289*). This parasite has, besides, been observed frequently to insert its ovipositor into a larva in which dissection or rearing showed that no egg had been deposited. A number of specimens of *Alsophila pometaria* Harris were apparently oviposited in by *M. versicolor*, but no parasite was obtained on rearing, which was somewhat surprising, since the parasite has been recorded in Europe from *Eupithecia exiguata*, which also is one of the geometrid subfamily Hydriomeninae. Caterpillars of *Phigalia titea* Cramer (a geometrid), of *Xylina antennata* Walker (a noctuid), and of several species of Tortricidae, as well as larvæ of a tenthredinid, were apparently oviposited in, but rearing and dissection showed that no eggs had been deposited. When even a membracid nymph was introduced into a vial containing a female of *M. versicolor*, the parasite advanced toward the hemipteron with ovipositor projecting forward between the front legs. Evidently *M. versicolor* often attacks from some motive other than that of oviposition.

There is unquestionably at least a partial third generation on various native hosts, particularly upon the species of Hemerocampa, Notolophus, Hyphantria, and other closely allied forms, early stages of which are in

the field during July. The adults of this generation, together with those of the other generations that have lived over, oviposit in the small brown-tail-moth caterpillars during the early autumn. The adults of *M. versicolor*, particularly the females, are much more rugged than those of *A. lacteicolor*, and often live many weeks, even two or three months, so that occasionally females of the first generation may attack the small brown-tail-moth caterpillars in the fall.

ECONOMIC IMPORTANCE OF METEORUS VERSICOLOR

As a parasite of the hibernating brown-tail-moth caterpillars *M. versicolor* is much inferior to *A. lacteicolor*, destroying, on the whole, only a small percentage of them. On some occasions cocoons of *M. versicolor* have been found in enormous numbers in heavy brown-tail-moth infestations, but these cases are not common. Moreover, the parasitism upon the nearly full-grown brown-tail-moth larvæ is slight, and that upon native caterpillars appears to be almost insignificant. The reasons for the lesser importance of this parasite are probably in large part the dependency of the species upon the brown-tail moth for hibernation and the extremely heavy parasitism by secondaries. Fully 50 to 75 per cent of the cocoons of *M. versicolor* are parasitized by various chalcidoids and ichneumonids, which recalls Riley's note (*4, p. 532*) following his description of *Meteorus hyphantriae*, where he states that—

. . . of 450 cocoons collected 84 per cent were hyperparasitized.

Among the secondary parasites reared from *M. versicolor* were representatives of the following chalcidoid genera: Eupelmus, Spilochalcis, Dibrachys, Hypopteromalus; and of the ichneumonid genera Pezomachus and Hemiteles. Still another factor contributing to lessen the importance of the Meteorus is the failure of many larvæ to transform to pupæ after they have spun cocoons; the percentage of Meteorus cocoons which give forth neither primaries nor hyperparasites is very high. Furthermore, the larva of *A. lacteicolor*, whenever it occurs in the same hibernating brown-tail-moth caterpillar with *M. versicolor*, causes the death of the latter. All these checks upon its development and increase combine to make *M. versicolor* a parasite of lesser importance.

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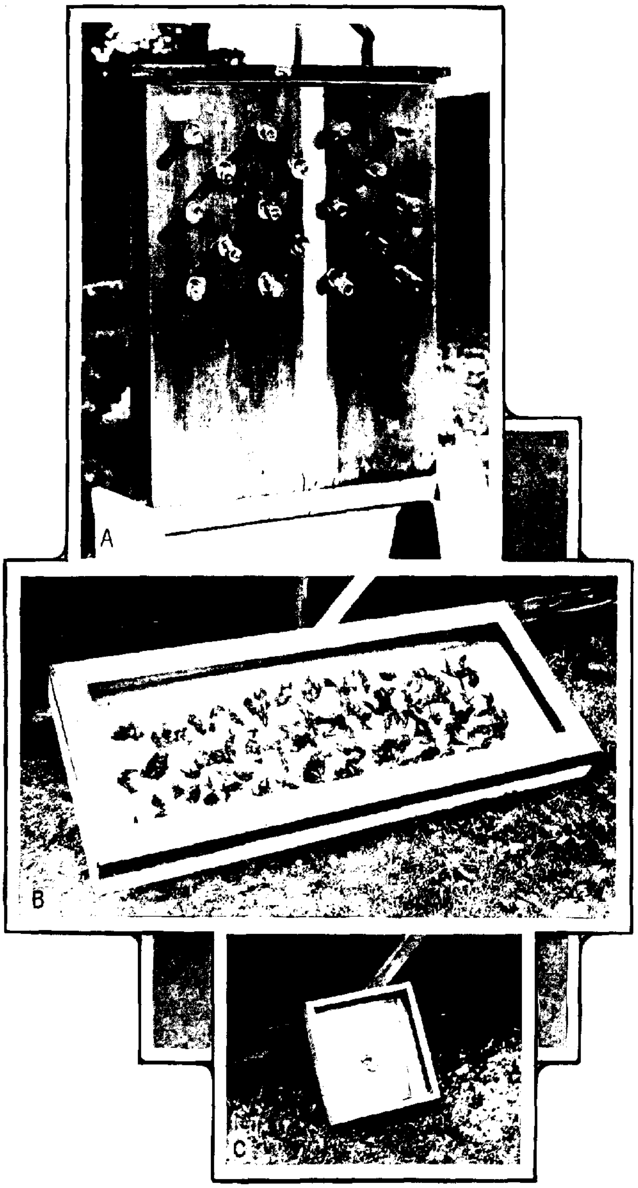
PLATE 19

A.—Large wooden cage used for rearing parasites from imported brown-tail-moth webs. (Designed by Messrs. Howard and Fiske.)

B.—Large rearing tray with cloth bottom, designed by Mr. W. F. Fiske, and used for rearing *Apanteles lacteicolor* and *Meteorus versicolor* from brown-tail-moth caterpillars. Webs are shown on bottom of tray.

C.—Small single-web rearing tray with paraffin-paper bottom.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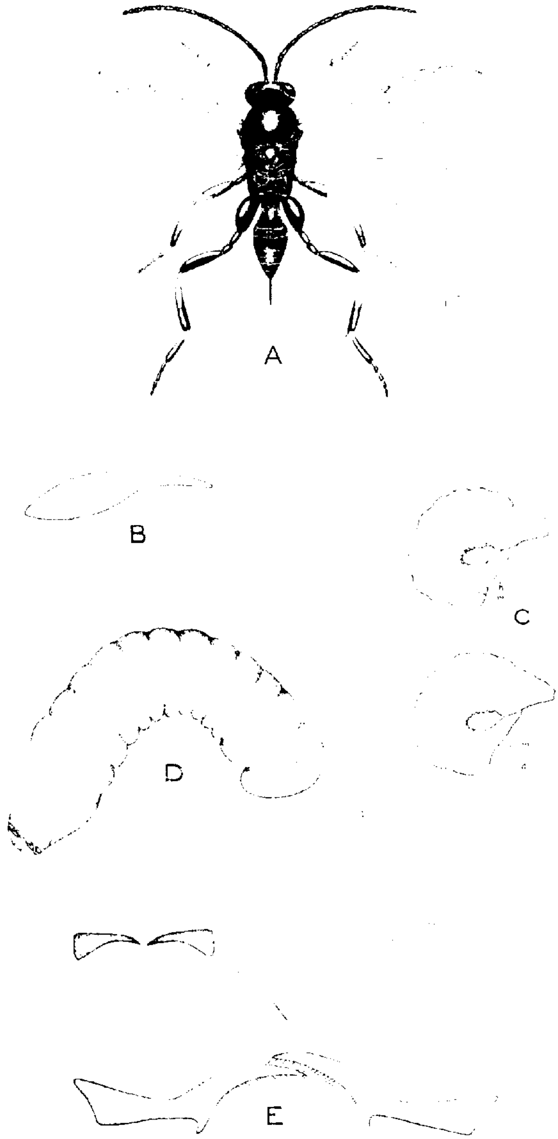
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PLATE 20

Apanteles lacteicolor:

A.—Adult female. Much enlarged.

B.—Egg. Much enlarged.

C.—Hibernating (first stage) larva, before (above) and after (below) evagination of hind intestine: *h*, Hind intestine; *m*, place of attachment of midintestine to hind intestine; *a*, anal vesicle. Much enlarged.

D.—First-stage larva after feeding in spring, ready to pass into second stage; dorsal view: *a*, Anal vesicle. Much enlarged.

E.—Larval mandibles: Upper left, first stage; upper right, second stage; below, third stage. The mandibles of first and third stages are chitinized; those of the second stage not chitinized. Much enlarged.

PLATE 21

A.—*Apanteles lacteicolor:* Third-stage larva. Anal vesicle still present. ×5.

B.—*A. lacteicolor:* Pupa. ×5.

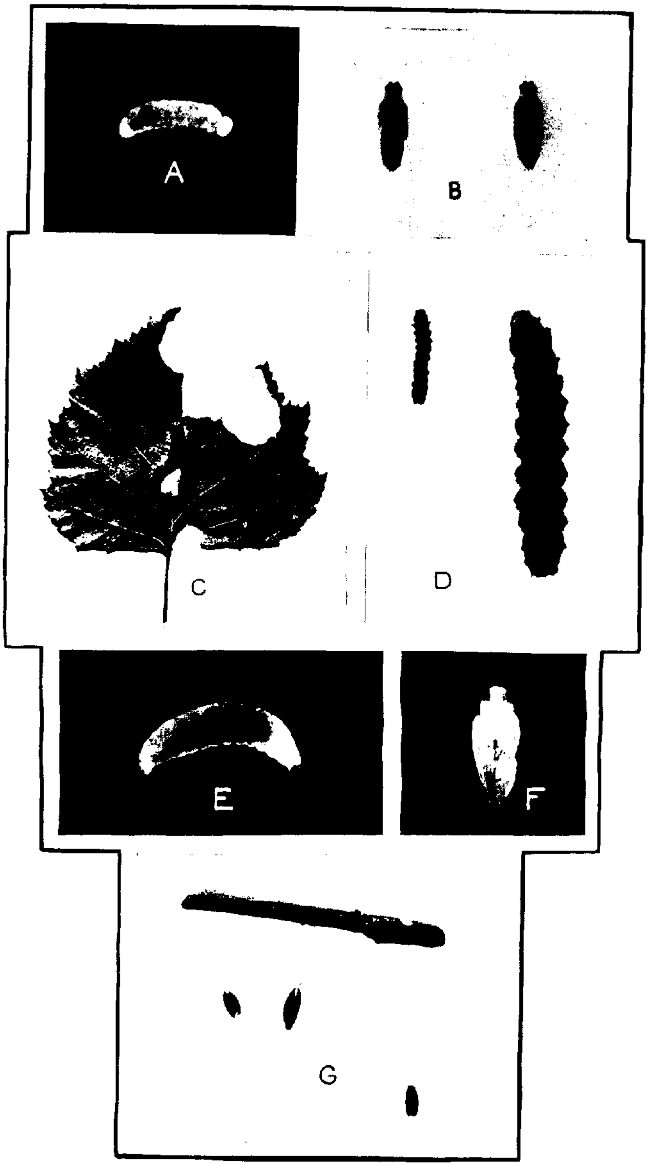
C.—Third-stage gipsy-moth caterpillar with cocoon of *A. lacteicolor.* Natural size.

D.—Two larvæ of an undetermined arctiid from the same egg mass: Above, parasitized by *A. lacteicolor;* below, unparasitized. ×2.

E.—*Meteorus versicolor:* Third-stage larva. ×5.

F.—*M. versicolor:* Pupa. ×5.

G.—*M. versicolor:* Cocoons. Natural size.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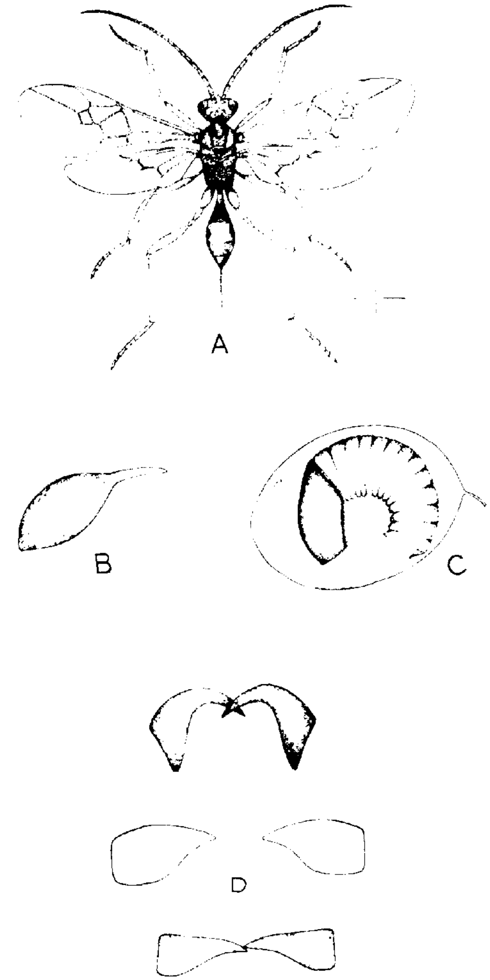
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PLATE 22

Meteorus versicolor:

A.—Adult female. Much enlarged.

B.—Egg. Much enlarged.

C.—Larva ready to issue from egg. Much enlarged.

D.—Larval mandibles: From top to bottom, first, second, and third stages. The mandibles of first and third stages are chitinized; those of the second stage not chitinized. Much enlarged.

A HITHERTO-UNREPORTED DISEASE OF OKRA

By L. L. Harter

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INTRODUCTION

In the summer and fall of 1916 officials of the Office of Seed and Plant Introduction called the writer's attention to a disease of okra pods [*Abelmoschus esculentus* (L.) Moench.] found at the Yarrow (Maryland) Field Station of the Department of Agriculture. Later in the season material was brought in from the same place by Dr. B. T. Galloway, of the Bureau of Plant Industry, who reported considerable damage to the pods. In fact, the disease was so general and destructive that a comparatively small percentage of a full crop of healthy seed was harvested. The seed from the 1916 crop was not used either for distribution or for replanting, but a small amount of it was turned over to the writer for examination and experimental work.

The seed from which the diseased plants were grown had come originally from three different sources. One importation, SPI [1] 27810, came originally from Erivan, Caucasus, Russia, in 1910, and was planted at Yarrow for the first time in 1913 and was grown there each succeeding year up to and including 1916. While a part of the original seed was sent elsewhere to be grown, none of the seed grown at these other places was brought to Yarrow. Another importation, SPI 34165, from Lucknow, India, was received in 1912 and grown at Yarrow from 1913 to 1916. A third importation, SPI 41724, from Athens, Greece, was received in 1916 and grown there only one year (1916).

It is possible that this disease was imported with the seed from Russia, India, or Greece, since no reports of such a disease have been found from Maryland. That it can be carried on the seed is evident, from the fact that the causal fungus was isolated several times from seed collected from diseased pods, both before and after surface disinfection. In 1878 Cooke [2] describes a new species of Phoma, *Phoma okra*, on stems of okra collected by Ravenel in South Carolina. Similar material bearing a fungus attributed to the same species of Phoma was collected by Langlois in 1886 and again in 1887. The writer has examined Cooke's type material of *Phoma okra* as well as the specimens, and no septate spores were found.

In 1908 Barrus collected stems and pods of okra in the State of New York bearing a fungus which he identified as *Phoma okra* Cke. Some

[1] SPI=Office of Seed and Plant Introduction No.

[2] Cooke, M. C. North American fungi. *In* Hedwigia, Bd. 17, No. 3, p. 37-40. 1878.

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of this material was deposited in the pathological collections of the Bureau of Plant Industry, United States Department of Agriculture, and upon examination a large percentage of the spores were 1-septate. Spore measurements and other characters show it to be identical with the organism with which the writer has been working. This fungus therefore was present in this country before the importations mentioned above were made. In the light of these facts it is impossible to state definitely the source of infection. Either the fungus may have been imported with the seed or the infection of these plants may have originated from domestic sources.

DESCRIPTION OF PODSPOT

This disease has not been found to affect the leaves under natural conditions, and leaves sprayed with a suspension of the spores in water were not infected. Spots similar to those on the pods (Pl. 23, A) are found on the limbs (Pl. 23, B), but the damage there is relatively small. The greatest injury is done to the pods, and for that reason the common name "podspot" is proposed for this disease.

The causal organism grows rather slowly in the host tissue. There is little or no evidence of infection for a week or so after inoculation, but soon after that time a dark band, somewhat watersoaked in appearance, appears around the point of inoculation. From this time on development is a little more rapid, and a spot ½ to 1 inch in diameter results at the end of two or three weeks. Numerous pycnidia appear at about this time in the dead tissue. They continue to increase in number and to form in a more or less concentric manner as more host tissue is killed. On the death of the pod, pycnidia may or may not develop indiscriminately over the entire surface.

The spots are oval to oblong in shape, the longest diameter being the long way of the pod. The fungus follows the course of the fibrovascular bundles, and often the bundles may be found invaded and blackened some distance in advance of any evidence of the fungus on the surface. The fungus eventually grows through the pod, into and among the seed. Pycnidia were found on the seed, and the fungus was isolated from the seed after thoroughly washing and disinfecting the surface.

CAUSE OF OKRA PODSPOT

Isolations from diseased pods have always yielded a fungus bearing the characteristics of one of the Sphaeropsidaceae. Diseased pods and stems were wintered out with the hope that a perfect stage of the organisms might develop. However, even as late as June the same imperfect fungus was isolated from the old pods. Until more is known of the life history of the fungus it will be referred to the form genus Ascochyta (*A. abelmoschi*, n. sp.) and tentatively described as follows:

Ascochyta abelmoschi, n. sp.

Spots somewhat circular, often with a brown to black margin, more or less distinctly zonate; pycnidia gregarious, often crowded together, brown to black, lenticular, pyriform to globose, rather thick walled, at first buried, becoming finally erumpent, 65 to 225 μ in diameter, ostiolum small, mostly central; pycnospores, cylindrical to oval, straight or curved, 4.0 to 14.0 by 2.1 to 4.5 μ, hyalin, 1-celled for a long time, finally septating transversely at the center, then or not at all slightly constricted, rounded at the ends, when guttulate 2 to 4.

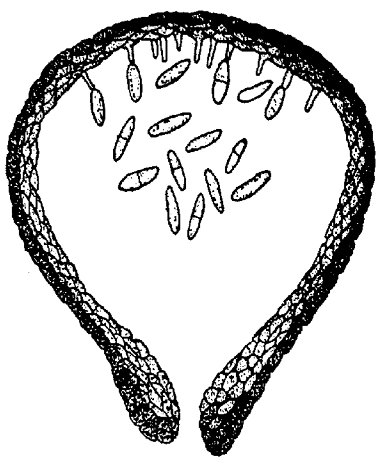


FIG. 1.—*Ascochyta abelmoschi:* A section through a pycnidium on the host showing the outer and inner walls, the sporophores and pycnospores. × 500.

Type specimens are deposited in the herbarium of the Pathological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

While the pycnidia are relatively small when on the host, they are very much larger and more variable in shape when grown in artificial cultures.

The pycnidium is inclosed in an outer darkwall about one or two cells in thickness (fig. 1). Within this is a somewhat thicker hyalin layer from which the rather stout blunt conidiophores arise (fig. 2). The ostiolum arranged centrally on the host is variously placed when the fungus is grown in artificial cultures. It is small, slightly drawn out, and the pycnidial walls surrounding it are slightly thicker and darker than at other parts of the pycnidium.

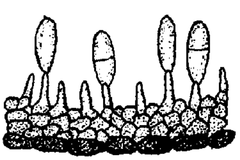


FIG. 2.—*Ascochyta abelmoschi:* A portion of the pycnidium shown in figure 1. × 1,000.

The spores (fig. 3), produced in great numbers, are hyalin and for a long time 1-celled. In old cultures and in the later stages of the development on the host some of the spores lay down a septum near the middle. Different specimens, as well as different cultures, vary as to the percentage of 2-celled spores, but no case has been found where more than 50 per cent of the spores have septated.

The spore may or may not be constricted at the septum. The spores of various forms, differing greatly in type, are straight or curved, and often larger at the ends than at the middle (fig. 3).

INOCULATION EXPERIMENTS

Podspot was reproduced with the characteristic symptoms on several varieties of okra and the organism recovered. It was again reproduced by inoculation from cultures resulting from such reisolations.

The original cultures were obtained in the fall of 1916, but the first inoculations were not made till some months later. Since okra does not grow well during the winter months under greenhouse conditions, plants were not started there till the spring of 1917. About August 1 abundant pods on these plants were suitable for inoculation. On August 10 a number were inoculated by inserting spores and hyphæ into wounds made with a dissecting needle. A few infections resulted from the inoculations, and the characteristic symptoms of the disease were produced. That a larger percentage of infection did not result was found later to be due to the fact that the pods were in most cases too mature when inoculated, young pods being much more susceptible. On August 15, pods in different stages of development, of five different varieties, New Lady Finger, Perkins Long Pod, Kleckleys Favorite, Dwarf Prolific, and White Velvet, were inoculated outdoors at the Arlington Experimental Farm as above with the same organism. Over 70 per cent of these pods developed the characteristic symptoms of the disease, the older pods remaining healthy or showing only slight infection. On August 20, pods, one-third to full grown but not mature, were inoculated in the greenhouse and 65 per cent became infected.

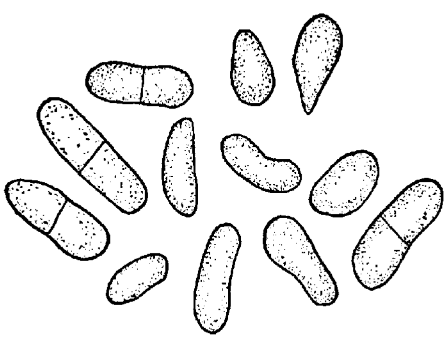


FIG. 3.—*Ascochyta abelmoschi:* A number of pycnospores, some of which are septated, showing the variations in shape and size. × 2,000.

The organism was recovered from the infected pods of the first inoculation and when fruiting abundantly was used in the greenhouse to inoculate pods in all stages of development. In some cases several pods on the same plant were inoculated. The results showed that the upper or younger pods were the first to show symptoms of the disease, and the spots enlarged more rapidly. The infected spot on the pod next below developed more slowly, while the pods lowest down on the stem either remained healthy or showed but slight evidence of disease and then only at the wound.

At the same time that this last pod experiment was carried out, leaves were sprayed with spores suspended in water, but no infection resulted. Since infected leaves were never found on diseased plants under field conditions, and spraying under artificial conditions yielded negative results, it is believed this is a disease of the pods and stems only.

Apparently several varieties of okra are susceptible to podspot. Infection takes place under natural conditions probably only when the pods are young, since old or nearly mature pods when wounded or inoculated usually resisted the fungus or showed but a slight indication of infection about the wound.

CULTURAL CHARACTERS

Ascochyta abelmoschi can readily be isolated in pure culture by the poured-plate method after a thorough washing of the infected pods, followed by surface disinfection in mercuric chlorid. It grows well on most of the agars, stems of *Melilotus alba*, cooked Irish potato cylinders, steamed rice and steamed corn meal. The maximum mycelial growth is made on agars and the minimum on Melilotus stems. On the other hand, it fruits sparsely on agars and abundantly on stems of *M. alba*. Growth is noticeable on most any of the media in common use in 24 to 48 hours at laboratory room temperature. On steamed rice and on steamed Irish potatoes an ocherous color appears in 48 hours and increases in intensity for several days. This color later gives way to a dirty ocherous color brought about largely by the development of the pycnidia.

Pycnidia develop not at all or sparingly on most of the agars. On stems of *Melilotus alba* they begin to appear in three days and to exhude spores in seven days. Pycnidia develop on rice and Irish potato cylinders in about three to four days and exhude spores in about eight days. Stems of *M. alba*, cooked rice, and Irish potato cylinders are good media for the growth of the fungus.

SUMMARY

(1) *Ascochyta abelmoschi* is parasitic upon the stems and pods of several varieties of okra.

(2) The disease caused considerable loss where it occurred in Maryland in 1916.

(3) The disease also occurs in New York State.

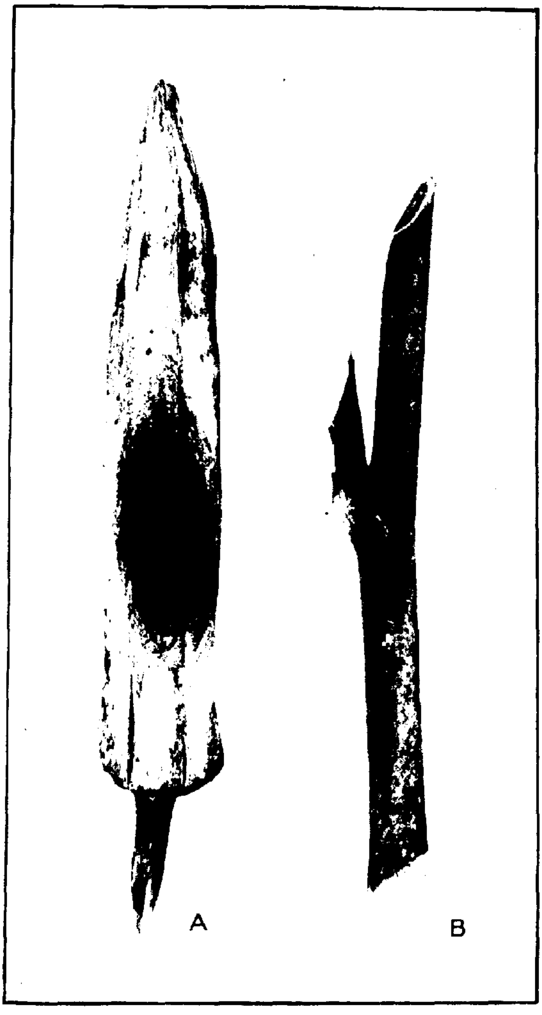
(4) The origin of this disease in Maryland is doubtful. Either it may have been imported with the seed or it may have originated from domestic sources.

(5) The fungus grows well on most any of the culture media in common use, but fruits the best on stems of *Melilotus alba* and cooked rice.

PLATE 23

A.—A pod of okra collected at Yarrow, Md., showing a typical spot caused by *Ascochyta abelmoschi*. The spots are usually more or less elliptical in shape and the pycnidia zonately arranged.

B.—A typical podspot infection on the stem of okra.


A
B

POTATO-STEM LESIONS

By H. A. Edson, *Pathologist*, and M. Shapovalov, *Agent, Cotton, Truck, and Forage Crop Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

The brown canker-like areas occurring on the underground portions of the potato (*Solanum tuberosum*) plants in various parts of the country have been attributed by many writers to the attacks of *Rhizoctonia solani* Kühn. (Rolfs,[1] Morse, and Shapovalov,[2] Drayton,[3] and others.) On the other hand, Link[4] has found that similar lesions on potato stems in Nebraska may be due to species of Fusarium. Observations during the last few years, as well as numerous isolations and inoculation experiments, show quite conclusively that although Rhizoctonia and Fusarium may constitute the two principal genera of fungi responsible for the injuries in question, yet at the same time there are undoubtedly several other organisms hitherto not connected with this trouble which are capable of producing similar and even macroscopically identical stem lesions. The relative importance and frequency of the individual members of this group may vary throughout the country with the changing soil, season, and climate.

EXPERIMENTAL WORK

ISOLATIONS

A great number of isolations were made in the summers of 1916 and 1917 from the material collected on various farms in northern Maine. Both severely injured stems and stolons and those showing only small individual lesions served as material for this work. The majority of the cultures yielded *Rhizoctonia solani* and *Fusarium oxysporum*, then followed *F. discolor*, *Botrytis* sp., *Alternaria solani*, *Alternaria* sp., *Clonostachys* sp., *Acrostalagmus* sp., *Sclerotinia* sp. and a number of Hyphomycetes which failed to show parasitism in subsequent inoculation experiments. Different lesions on the same plant frequently yielded different fungi and, in several instances two parasites developed in cultures

[1] Rolfs, F. M. POTATO FAILURES. A PRELIMINARY REPORT. Colo. Agr. Exp. Sta. Bul. 70, 20 p., 12 pl. 1902.

—— POTATO FAILURES. A SECOND REPORT. Colo. Agr. Exp. Sta. Bul. 91, 33 p., 5 pl. 1904.

[2] Morse, W. J., and Shapovalov, M. THE RHIZOCTONIA DISEASE OF POTATOES. Maine Agr. Exp. Sta. Bul. 230, p. 193–216, fig. 61–73. 1914. Literature cited, p. 216.

[3] Drayton, F. L. THE RHIZOCTONIA LESIONS ON POTATO STEMS. *In* Phytopathology, v. 5, no. 1, p. 59–63, fig. 5, pl. 6. 1915. Literature cited, p. 63.

[4] Link, G. K. K. A PHYSIOLOGICAL STUDY OF TWO STRAINS OF FUSARIUM IN THEIR CAUSAL RELATION TO TUBER ROT AND WILT OF POTATO. *In* Bot. Gaz., v. 62, no. 3, p. 169–209, 13 fig. 1916. Literature cited, p. 207–209.

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from a given lesion. In the spring of 1918 several specimens were obtained from Florida, some of which had characteristic brown lesions on the stems. Plantings made from these diseased areas yielded pure cultures of *F. oxysporum*. Identical results were also obtained with some of the material collected recently in the vicinity of the District of Columbia.

INOCULATIONS

Although certain preliminary tests were made in the field, this work was carried on chiefly under greenhouse conditions at Washington, D. C., with disinfected seed and steam-sterilized soil and pots, watered from the city mains supplied with clarified and filtered Potomac River water. The following method of inoculation has been found very satisfactory: When the young plants were about 2 or 3 inches high, the soil was removed at one side of the plant clear down to the seed piece (on the average, about 2 inches from the surface of the soil), care being taken to avoid as much as possible any injury to the epidermis of the stem. Then the culture was removed from the test tube on a piece of clean absorbent cotton, and the preparation was placed on the exposed side of the stem. Each fungus had been grown for this purpose on three kinds of medium; rice, cooked potato cylinders, and melilotus stems. Finally the soil was replaced and heaped up about the plant, nearly covering it. Control plants were treated in a similar way except that sterile culture medium instead of fungus cultures was applied to the stems. About four weeks after inoculation the plants were carefully dug, washed, and examined. Besides the fungi isolated from the potato, a number of Rhizoctonia strains[1] from various other hosts, as well as authentic cultures of several species of Fusarium, were included in the tests. The combined detailed results of these experiments are given in Table I.

TABLE I.—*Results of the potato-stem inoculations with Rhizoctonia solani, Fusarium spp., and several other fungi*

Name of culture.	Date of isolation.	Number of plants inoculated.	Number of plants infected.	Character of injury produced.
Rhizoctonia solani (*R. potomacensis* Wollenw. from tomato).	August, 1912...	8	8	Irregular, deep, dark-brown lesions on stems; stolons and new tubers also affected.
R. solani, R. Kan. (from beets).	1913..........	5	3	Brown discoloration at the base of the stems.
R. solani, R. S. (from beet seedlings).	July, 1912.....	5	3	Large brown canker in one case and a slight russetting in two others.

[1] The word "strain" in its application to Rhizoctonia is used in the present paper merely to differentiate cultures obtained from different hosts or from the same host from different localities. It does not imply any reference to their taxonomic relationships.

TABLE I.—*Results of the potato-stem inoculations with Rhizoctonia solani, Fusarium spp., and several other fungi*—Continued

Name of culture.	Date of isolation.	Number of plants inoculated.	Number of plants infected.	Character of injury produced.
R. solani, Hyp. I (from potato).	October, 1914	8	5	A number of medium-sized deep and very dark cankers on stems.
R. solani, R. V (from beet seedlings).	September, 1911.	5	0	....
R. solani, R. VI (from beet seedlings).	.....do........	8	8	Large, deep, irregular, medium-dark necrotic areas on stems.
R. solani, R. VII (from beets).	October, 1911	6	6	Numerous small dark-brown spots on stems; brown discoloration on roots present.
R. solani, R. XI (from potato).	October, 1912	8	8	Dark-brown cankers on stems and stolons.
R. solani, R. XII (from beets).	September, 1912.	8	6	Small, light-brown spots on stems.
R. sp., R. XIII (from onion).	May, 1911......	3	0	....
R. solani, R. XIV (from radish).	February, 1913.	3	0	....
R. solani, R. XV (from pine seedlings).	June, 1911.....	6	6	Small lesions on stems and some on stolons.
R. solani, R. XVI (from beets).	1912..........	5	2	Small brown spots on stems.
R. solani, R. XVII (from peanut).	1914..........	5	3	Do.
R. solani, R. XVIII (from potato).	October, 1914	3	3	Do.
R. solani, R. XX (from potato).	1914..........	3	0	....
R. solani, R. XXIII (from alfalfa).	September, 1914.	3	3	Small dark-brown spots on stems; younger shoots and some of the roots killed.
R. solani, R. XXIV (from potato).	June, 1915.....	3	1	Large necrotic area on one stem.
R. solani, R. XXV (from carnation).	September, 1915.	5	2	Brown spots on stems.
R. solani, R. XXVI (received from Amsterdam).	1916..........	3	2	Large irregular lesions on stems; some infection on stolons present.
R. solani, R. XXVII (from potato.)	1916..........	3	0	....
R. solani, R. XXIX (from potato).	July, 1916.....	4	2	Brown lesions on stems.
R. solani, R. XXX (from potato).	July, 1916.....	4	3	Deep cankers on stems.
R. solani, R. 724 F (from pine).	1916..........	3	3	Pronounced depressed brown lesions; especially severe on stem inoculated with rice culture.
R. solani, R. 147 W (from spruce).	1910..........	3	3	Distinct but small and shallow spots on stems; more at the crown.
R. solani, R. 187 K (from potato).	1910..........	3	3	Only slight browning on stems.

TABLE I.—*Results of the potato-stem inoculations with Rhizoctonia solani, Fusarium spp., and several other fungi*—Continued

Name of culture.	Date of isolation.	Number of plants inoculated.	Number of plants infected.	Character of injury produced.
R. solani, R 186 L (from potato).	1910	3	2	No infection in case of melilotus culture and only slight browning on stems inoculated with rice and potato cultures.
R. solani, R. 361 L (from pine.	1915	3	0	....
Fusarium coeruleum	March, 1915	3	3	Small dark lesions on stems, stolons, and roots.
F. discolor	1908	8	8	Lesions on stems and occasionally on roots; in two instances injury very severe (from rice culture), others only slight.
F. discolor var. *sulphureum*	June, 1909	3	3	Small lesions on stems and stolons.
F. eumartii	January, 1914	6	6	Serious stemrot in two instances; deep cankers on the remaining stems; lesions on roots and stolons.
F. oxysporum	October, 1916	8	8	Deep irregular, brown lesions on stems and occasionally on stolons.
F. radicicola	February, 1916	4	3	Deep dark-brown lesions on stems, stolons, and roots (melilotus culture produced no effect).
F. solani	February, 1914	3	0	Only slight discoloration.
F. trichothecioides	October, 1916	4	4	Very large dark, deep cankers on stems; lesions on on roots and stolons.
Alternaria sp. I	1916	5	5	Distinct brown necrotic areas varying in severity on different plants.
A. solani	1916	3	3	Large dark-brown cankers on stems.
Botrytis sp. I (from potato leaf).	1916	8	8	Distinct brown but shallow lesions on stems.
Botrytis sp. II (from potato stem).	1916	6	6	Severe dark-brown lesions on stems.
Sclerotinia sp. (from a sclerotium inside of stem).	1916	2	2	Do.
Zygorhynchus sp	1917	3	3	Shallow lesions on stems and stolons.
Corethropsis sp	1917	3	3	Shallow lesions on stems.
Phoma sp	1916	6	4	Superficial russeting only (on stems).
Acrostalagmus sp	1917	6	6	Irregular, brown, lesions on stems.
Clonostachys sp	1917	6	6	Irregular, light-brown, somewhat depressed lesions on stems.
Verticillium albo-atrum I (from eggplant).	September, 1915	3	3	Slight amount of russetting on stems.
V. albo-atrum (from potato).	1917	3	3	Slight discoloration of stems.
Verticillium sp. (from okra).	1917	3	3	Do.

In addition to the fungi listed above a miscellaneous group of apparently saprophytic organisms obtained in cultures made from potato stems was included. This group comprised species of Penicillium, Phoma, Chaetomium, and several unidentified fungi. Triplicate inoculations were made with each member of the group. In a few instances a faint brownish discoloration was observed on stems just beneath the cotton covering the inoculum; however, its amount was too insignificant to warrant a conclusion that any of these organisms were pathogenic. The most serious infection was secured with several strains of *Rhizoctonia solani*, *Fusarium eumartii*, *F. oxysporum*, *F. radicicola*, *F. trichothecioides*, *F. discolor*, *Alternaria solani*, *Botrytis* sp. from potato stem, *Sclerotinia* sp. from potato stem, *Acrostalagmus* sp., and *Clonostachys* sp. The character of injury produced by various fungi, as well as the appearance of the control plants and those inoculated with saprophytic species, is illustrated in Plates 24, 25, and 26. Control plants remained free from underground injuries with the exception of a few stems, when a slight browning such as was noted in case of some saprophytes was present (Pl. 26, I–L).[1]

The degree of parasitism of the different strains of Rhizoctonia varied from absolute absence of any visible injury to the formation of large and deep cankers. This phenomenon has been already noted by Rosenbaum and Shapovalov[2] with regard to their strains of this fungus. In the present work the evidence was even more striking. Not only the size and the depth of the lesions were unlike, but also their color and shape were quite peculiar to certain particular strains. Moreover, these characters were not incidental to one series only, but, on the contrary, with certain strains quite constant in every series of inoculation. For example, *Rhizoctonia potomacensis* Wollenw. always produced dark-brown and deep lesions, and similar injury resulted from R. XI and from R. 724 F, while R. VI invariably formed large, deep and medium-dark necrotic areas; R. VII and R. XXIII produced small dark spots, R. XII and R. 147 W small light-brown spots, and R. V., R. XIV, R. XX, R. XXVII, and R. 361 L in no case produced any injury whatever. With the remaining strains of Rhizoctonia the peculiarities were not so constant nor so distinct.

The virulence of the different strains did not appear to be correlated in any way with the length of time they had been carried in artificial culture or with the host from which they were originally isolated. Thus R. V and R. VI, isolated from sugar-beet seedlings in September, 1911, produced respectively, no injury and large, deep, irregular necrotic

[1] Certain greenhouse experiments conducted since the completion of this work indicate that *Penicillium oxalicum* also is able to produce distinct brown lesions on the potato stems inoculated with pure cultures of this fungus.

[2] ROSENBAUM, J., and SHAPOVALOV, M. A NEW STRAIN OF RHIZOCTONIA SOLANI ON THE POTATO. *In* Jour. Agr. Research, v. 9, no. 12, p. 413-419, 3 fig., pl. 25-26. 1917.

areas. R. XI, isolated from potato in October, 1912, R. XII, isolated from beets in September, 1912, R. XV, isolated from pine seedlings in June, 1911, and R. XXIII, isolated from alfalfa in September, 1914, uniformly yielded positive results, while R. XXIX and R. XXX, isolated from potato in July, 1916, gave positive results only in two out of four and three out of four cases, respectively, and R. XX, isolated from potato in 1914, and R. XXVII, isolated from potato in Europe and received from Amsterdam in 1916, were among the strains constantly giving negative results. Two other European strains employed, Hyp. I and R. XVIII, isolated from potato October, 1914, gave positive results five times out of eight and three times out of three, respectively. These two strains were isolated and contributed by Dr. Pethybridge, who stated that Hyp. I was obtained from a single spore of *Hypochnus solani* (*Corticium vagum*) developing on potato stems in Ireland. *Rhizoctonia potomacensis* Wollenw., which appears to differ in no way from *Corticium vagum* B. and C. and which was isolated from tomato in September, 1912, was one of the most aggressive strains employed. It was strongly parasitic on tomatoes and on sugar beets both as a damping-off fungus and in the production of rootrot of adult plants. Five strains were contributed by Mr. Carl Hartley, of the Bureau of Plant Industry, with data regarding their origin and virulence as damping-off agents on pine seedlings. Named in the order of diminishing virulence on potato stems they are R. 724 F from pine, strong but not maximum virulence on pine; R. 147 W from spruce, maximum virulence on pine; R. 187 K from potato, moderate to weak virulence on pine; R. 186 L from potato, nearly or entirely nonparasitic on pine; R. 361 L from pine, moderate to weak virulence on pine. The two strains most active on pine were also most virulent to potato stems but in reverse order; R. 187 K was mildly pathogenic to both hosts; while R. 361 L, mildly parasitic on pine, did not injure potato stems, and R. 186 L, nonparasitic to pines, was only very mildly pathogenic to stems.

Certain variation in the amount of infection was noted in connection with the viability of a particular organism in pure culture. Thus, for instance, as a rule, little injury, or none, resulted from inoculation with Rhizoctonia cultures grown on melilotus stems, which is not a very satisfactory medium for this fungus, while rice and potato cultures produced severe lesions.

The infection with *Fusarium eumartii*, *F. radicicola*, *F. trichothecioides*, both species of Alternaria, *Botrytis* sp. from stem, and *Sclerotinia* sp. from stem as a rule produced deep necrotic lesions, sometimes taking on the appearance of a dry stemrot. This was especially true with *F. eumartii* (Pl. 25, C–I). *F. oxysporum*, which in these trials did not penetrate the vascular elements, showed a distinct ability to attack violently other tissues of the potato stem. On the other hand, *F. trichothecioides*, after

penetrating the stem to a considerable depth, invaded the vascular bundles in one instance. Subsequently dark-brown discoloration developed and the organism was recovered in pure cultures from the petioles of the topmost leaves.

CONCLUSIONS

(1) Neither *Rhizoctonia solani* Kühn nor any particular species of Fusarium can be held as the sole agents responsible for the familiar stem and stolon lesions of the potato.

(2) Several parasitic species of Fusarium, as well as Alternaria, Botrytis Sclerotinia, Zygorhynchus, Corethropsis, Phoma, Clonostachys, Acrostalagmus, and probably other fungi, should be included with certain strains of Rhizoctonia in the group of the causal organisms.

(3) While this group of parasites may be quite large, a number of strains of Rhizoctonia, along with other saprophytic species, are associated with stem lesions which are unable to attack the underground portions of the potato plant.

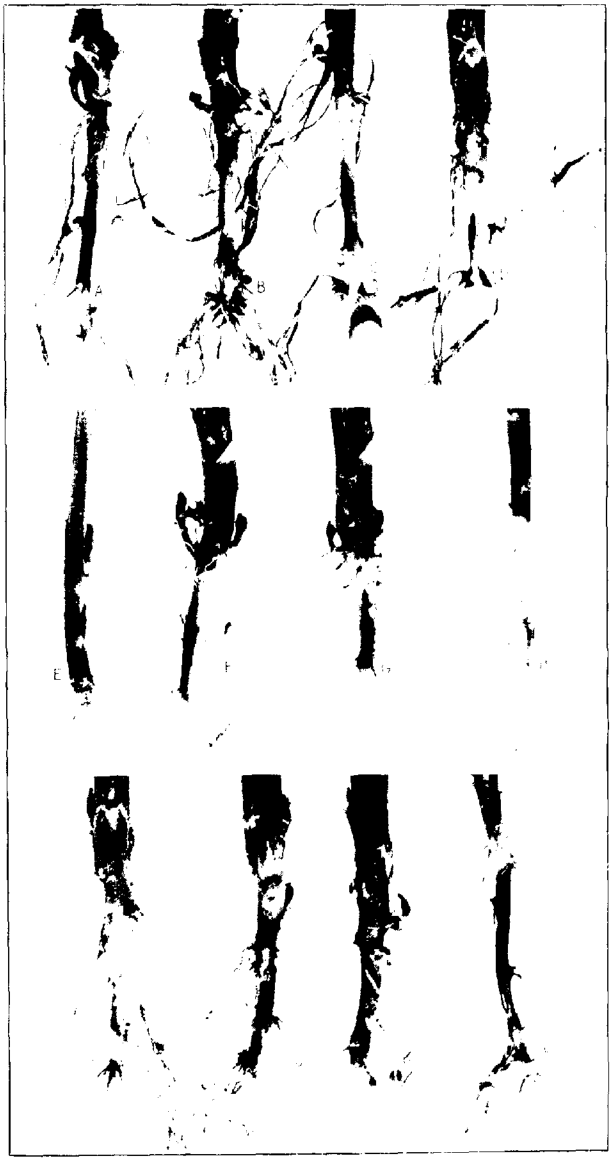
(4) The lesions produced by some of these fungi, while practically inseparable by their macroscopic characters when produced under natural field conditions, show distinct characteristics peculiar to certain strains or species when reproduced under control conditions in the greenhouse.

PLATE 24

Potato-stem lesions four weeks after inoculation:

A–H, Plants inoculated with *Rhizoctonia solani:* A, R. VII; B, C, E, *R. potomacensis;* D, Hyp. I; F, R. S.; G, R. VI; H, R. XVI.

I–L, Plants inoculated with species of Fusarium: I, *F. solani;* J, K, *F. radicicola;* L, *F. trichothecioides.*


A
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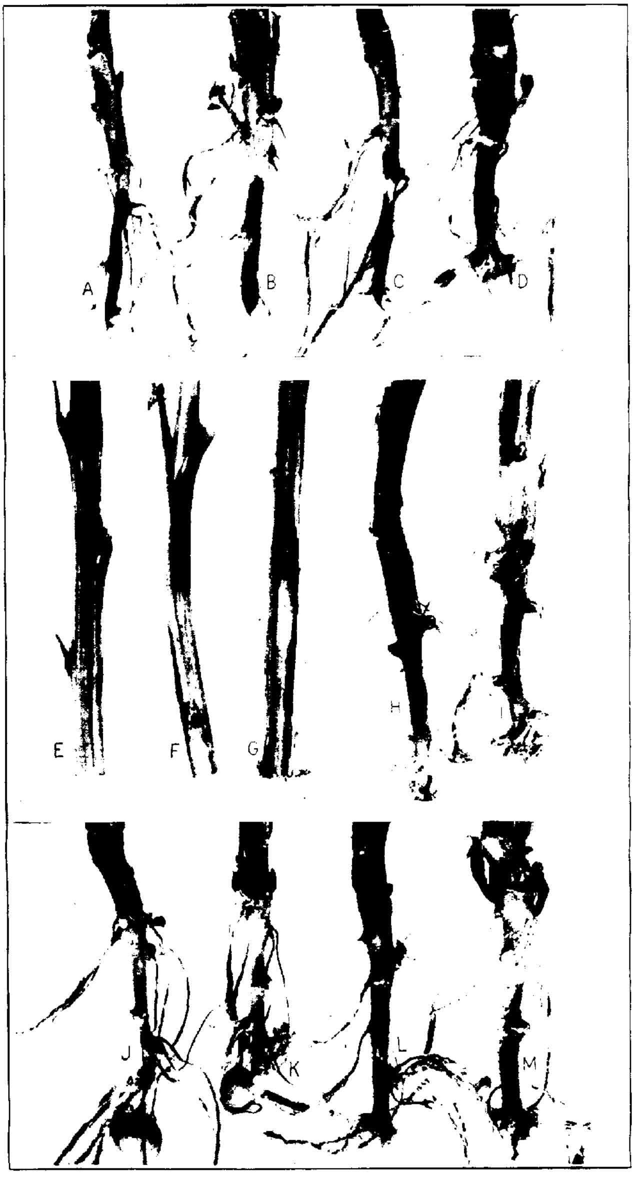
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PLATE 25

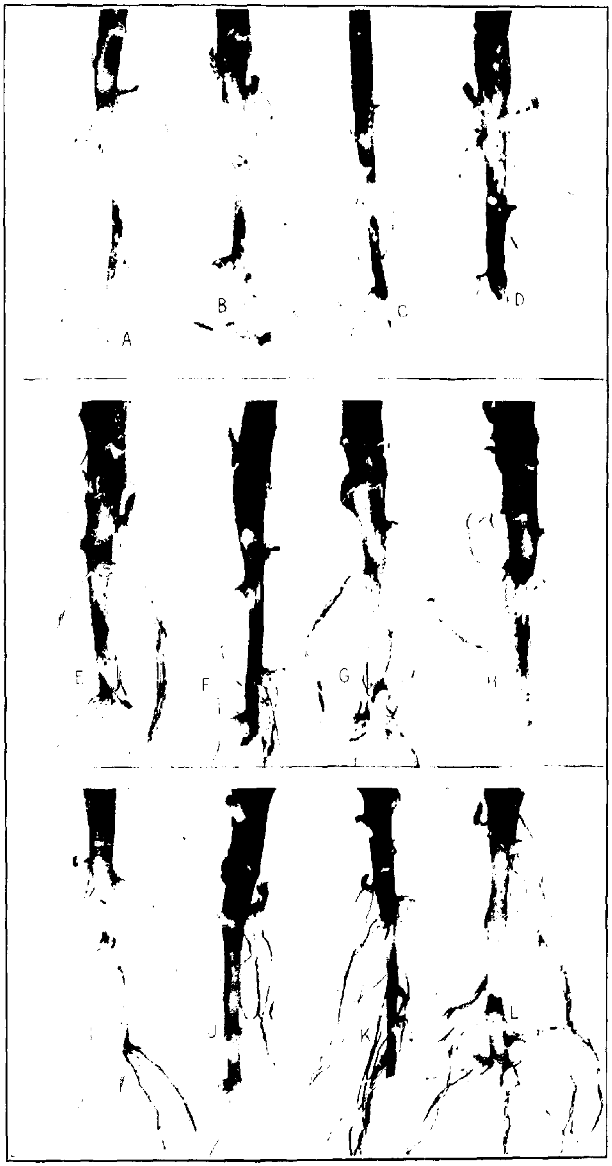
Potato-stem lesions four weeks after inoculation:

A-L, Plants inoculated with species of Fusarium: A, *F. discolor;* B, *F. oxysporum;* C-I, *F. eumartii;* E-H represent portions of the same plant, showing necrotic areas throughout the stem; J, *F. coeruleum;* K, *F. solani;* L, *F. discolor* var. *sulphureum.*
M, Plant inoculated with *Botrytis* sp. I.

PLATE 26

Potato-stem lesions four weeks after inoculation with miscellaneous fungi:

A, *Clonostachys* sp.;
B, *Zygorhynchus* sp.;
C, *Alternaria* sp. I;
D, *Alternaria (Macrosporium) solani;*
E, *Phoma* sp.;
F, *Corethropsis* sp.;
G, *Chaetomium* sp.;
H, *Acrostalagmus* sp.;
I–L, Control plants.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